XV. *On the Homologies and Succession of the Teeth in the Dasyuridæ, with an Attempt to trace the History of the Evolution of Mammalian Teeth in general.*

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Received April 4,—Read April 28, 1887.

[PLATES 27, 28.]

IN the year 1867 a paper* was contributed to the Royal Society by Professor FLOWER, "On the Development and Succession of the Teeth in the Marsupialia," a paper which became at once the standard authority on the subject, and in which it was shown conclusively that among the Marsupialia only one single tooth ever had a deciduous or "milk" predecessor, and that this tooth was one homologous throughout the order, and corresponding to the last premolar of the ordinary Placental Mammals.

This paper was followed by another,† in which fresh observations were recorded on the presence or absence of a tooth-change in the Marsupials and other Mammals, and notes made on the methods of tooth-notation in use—a subject which naturally arises out of all investigations into the homologies of teeth.

Finally, in the article "Mammalia" in the new edition of the 'Encyclopædia Britannica,'‡ the same author has given a summary of our present knowledge on the subject, to which I am indebted for much information and assistance.

In the course of preparing a systematic catalogue of the Marsupials in the Natural History Museum, my progress was soon arrested by the necessity of understanding and applying the very complicated homologies of the teeth, many points on which being by no means finally settled by Professor FLOWER, and the other publications on the subject being of a very vague and conflicting nature. The group wherein the greatest difficulty occurred was the Dasyuridæ, of which only one genus, *Thylacinus*, appears to have had its dental change properly described, and among whose members I have noticed several points that I believe to be worthy of publication, and from

* 'Phil. Trans.,' 1867, p. 631.

† "Remarks on the Homologies and Notation of the Teeth of the Mammalia," 'Journ. Anat. Physiol.,' vol. 3, 1869, p. 262.

‡ Ninth edition, vol. 15, 1883, p. 349.

the study of which I have been led on to form a theory on the evolution and succession of the teeth applicable to the Mammalia in general. This theory attempts to bridge over the existing gap between the Metatheria and Eutheria, and to show how the teeth of the one may have passed into those of the other.

Before commencing, I must express my sincere thanks to Mr. R. LYDEKKER, to whose extensive knowledge of Mammalian Palæontology and its literature I am largely indebted, and with whom every point in the present paper has been fully discussed—a sifting process which has, I hope, eliminated some of the unsound conclusions to which I might have otherwise come. Throughout the course of my work he has taken considerable trouble in obtaining information on various points, and this he has at all times freely communicated to me. I feel, therefore, that he should be credited with a very large share in the results, whatever their value may be, that are put forward in the present paper. I must also record the obligations I am under to Professor FLOWER himself, whom I have consulted on several points, and who has freely given me the benefit of his large knowledge on the subject.

To confine our attention, first, to the Dasyuridæ. In this family we find the greatest amount of variation in the extent to which the change of teeth takes place, some species having a well-developed successional tooth preceded by an equally well-developed milk-molar, while, on the other hand, others have no successional tooth at all, either in the milk or permanent stage. In this family also occurs *Myrmecobius*, remarkable for being the only known heterodont Mammal normally possessing more than four true molars.

This family has also another and more vital interest for the evolutionist, arising from the presumption that it was in all probability the family in which the change from Metatherian to Eutherian occurred. This presumption is based partly on the very generalised character of the family as a whole compared to the other and more specialised groups of Marsupials, but chiefly on the strikingly exact resemblance existing between the structure of the teeth of many of its members and that found both in certain of the "Creodonta" or Carnivora Primigenia, among which it is generally supposed that the direct ancestors of the modern Carnivora should be sought for,* and also in many of the more generalised Insectivora, whose claims to the parentage of other Placentals have been advocated by Professors HUXLEY,† PARKER,‡ and others.

The family Dasyuridæ consists of the following genera, the respective numbers of their premolars and molars being placed after each :—

* See R. LYDEKKER, 'Catalogue of the Fossil Mammalia in the British Museum,' Part 5, 1887, pp. 26 (footnote) and 307.

† 'Zool. Soc. Proc.,' 1880, p. 657 and elsewhere.

‡ 'Phil. Trans.,' 1885, p. 268. 'Mammalian Descent,' 1885, p. 125 *et seq.*

	Premolars.	Molars.
Thylacinus	3	4
Sarcophilus	2	4
Dasyurus	2	4
Phascologale	3 (rarely 2 below)	4
Sminthopsis*.	3	4
Antechinomys	3	4
Myrmecobius.	3	5 or 6

Nothing of importance seems to have been published as to the tooth-change in any of these genera, with the exception of *Thylacinus*, worked out by Professor FLOWER. This animal has its successional tooth, or "pm^4,"† preceded by a distinct milk-molar, which is, however, never functional, and falls out exceedingly early.

In *Dasyurus* and *Sarcophilus* neither of the two premolars has a milk predecessor, and, owing to this, their homologies have not been finally determined, although Professor FLOWER has acutely suggested,‡ judging only from KREFFT's description § of his "*Chætocercus cristicauda*," that it is the last, and usually changing, premolar which has disappeared, a suggestion which I am now in a position to prove entirely true.

On *Sminthopsis* and *Antechinomys* I propose to make no remarks, as their dentition is palpably the same as that of the common members of the genus *Phascologale*, on which my chief observations have been made, and from which I shall afterwards return to *Dasyurus* and the other members of the family.

In *Phascologale* the shape and size of the two anterior permanent premolars are always very constant, but the third and last, or pm^4, presents us with a remarkable series of gradations in size, gradations which prove that it is undoubtedly this tooth that has altogether disappeared in *Dasyurus* and *Sarcophilus*. These gradations do not need detailed description here, especially as the figures (Plate 27, figs. 1–5) show them far more intelligibly than any description could do. It is sufficient to say that in certain species, such as *Phascologale virginiæ* and *penicillata* (figs. 1 and 2), the tooth is larger and longer than pm^3, and that from this size a perfect set of gradations exists, down to the minute and practically functionless tooth found in *Ph. apicalis* (fig. 4), while in two species even, *Ph. cristicaudata* and *thorbeckiana*, the tooth is often altogether absent in the lower jaw.

* = *Podabrus*, GOULD, *auctorum*.

† This tooth, being the homologue of the fourth premolar of other Mammals, should evidently be called by the same name, viz., pm^4, whatever the actual number of premolars, and therefore its serial position, may be.

‡ 'Journ. Anat. Physiol.,' vol. 3, p. 277.

§ 'Zool. Soc. Proc.,' 1866, p. 435.

As to the milk dentition, those species that have a large permanent pm^4 have a distinct tricuspid milk-tooth preceding it (Plate 27, fig. 6), and persisting until a comparatively late period of life.* On the other hand, when the permanent pm^4 shows a tendency to disappear, the milk-tooth would seem to be first gradually aborted; thus in *Ph. doriæ*, where the permanent tooth is of a medium size, the milk-tooth is quite minute and functionless, while in the still smaller-toothed *Ph. apicalis*, and also in *Ph. wallacei*, I have been unable to find any trace of a milk-tooth in the only young specimens available—the permanent tooth, however, as in the other species, still rising into its place considerably later than any of its neighbours. The actual calcification of this tooth seems also to take place much later in *Phascologale* than in any other of the tooth-changing Marsupials, so that the tooth is often not to be found beneath the bone until a very short time before its eruption.

From these observations it is clear that the normal state of a member of the present group is to have three well-developed premolars, the last one of which has a milk predecessor. Then a tooth-reduction has taken place, all of which has fallen on what is evidently a peculiarly plastic tooth, viz., pm^4, and this, with the milk-tooth preceding it, has been decreased in various degrees, and in the end altogether suppressed, as in the allied genera *Dasyurus* (Plate 27, fig. 5) and *Sarcophilus*.

Having thus found out which of the three premolars present in *Phascologale* has disappeared in *Dasyurus* and *Sarcophilus*, we have, before we can settle the proper homologies of even these three, to discover which of the full number of four premolars, still possessed by the Eutheria, has disappeared in *Phascologale* and other Marsupials, for it has always been the natural presumption that four, and not only three, was the original typical number of premolars as much among the Marsupial as among the Placental Mammals.† Since no species now living, however, shows this number, that presumption has hitherto remained unproved, and still less has it been proved which one of the full set of four has disappeared to leave the common number of three, most authors jumping to the conclusion that, as in so many Carnivora, it is pm^1 that has been suppressed. Now, however, I am at last able to prove the first, and make out the second point to my own satisfaction, and to that of both Professor FLOWER and Mr. LYDEKKER.

When looking at a somewhat abnormal skull of *Dasyurus maculatus*, I was struck by seeing a minute projection attached to the gum, *between the two premolars*, and, being on the look-out for such a thing, I immediately suspected that it might be the

* The specimen of *Ph. penicillata* with milk dentition, from which the figure is drawn, has its third molar up and in place, and has a basal length of nearly 40 mm. as compared to about 45 mm. in fully adult specimens.

† Although some even of the highest authorities look upon three as the typical or parent number of premolars in the Marsupials; see, for example, TOMES' 'Dental Anatomy' (2nd ed.), 1882, p. 420, where, apart from this point, a most excellent account is given of the structure and development of Marsupial teeth.

missing premolar, present through atavism. I then turned to *Phascologale,* in which, as pm^4 is still retained, there seemed more hope of tracing the other missing premolar; but here, in all the commoner species, the teeth fit so closely against one another that a functionless atavistic tooth would have no chance of developing. In certain of the rarer Papuan species, however, the teeth, owing to the length of the muzzle, are more separated from one another, and, on examining all the available examples of these, I was rewarded by finding on one side of the upper jaw, in a specimen of *Ph. dorsalis* belonging to the Genoa Museum,* a large and distinct tooth (Plate 27, fig. 7) protruding from the gum between the teeth corresponding to the two anterior premolars in an ordinary *Phascologale,*† and in exactly the same position, therefore, as the minute rudiments previously found in *Dasyurus.* The tooth itself is two-rooted, precisely similar in shape to the other premolars, and is of about half the size of the first premolar in the same species. This, then, was clearly the missing premolar, and that here was its most natural place is shown by the extreme frequency with which a marked and prominent gap exists at this point in adult Marsupials, as, for example, in *Didelphys, Perameles,* and others.

That the original typical number of premolars in the Mammalia was four is also strikingly exemplified by several of the earlier fossil Marsupials—as, for example, by *Triconodon,* which has the full cheek-teeth formula of four premolars and four molars; by *Ctenacodon, Plagiaulax minor,* and others; thus proving beyond question that the pm^2 discovered in the recent *Phascologale* is really an atavism and not a mere meaningless abnormality.

It results from this discovery as to the position of the missing premolar that in all the numerous Polyprotodont‡ Marsupials with three premolars these are homologous with the first, third, and fourth of the normal Mammalian dentition, and not with the second, third, and fourth, as has ordinarily been presumed to be the case.

For the abnormal specimen of *Phascologale dorsalis* we therefore obtain (on one side only) the following premolar formula :—P.M. $\frac{1\,.\,2\,.\,3\,.\,4\S}{1\,.\,0\,.\,3\,.\,4}$, from which the suppression of the upper pm^2 gives us P.M. $\frac{1\,.\,0\,.\,3\,.\,4}{1\,.\,0\,.\,3\,.\,4}$, the formula in *Thylacinus, Phascologale,*

* For the loan of which, and of a large series of other Papuan specimens, I have to thank my friend, the Marquis G. DORIA, Director of that Museum.

† Compare the teeth of the other side in the same specimen (Plate 27, fig. 8, reversed) for the correspondence between the different premolars.

‡ As to the Diprotodonta with three premolars, although, on the one hand, in the Mesozoic Plagiaulacidæ it was clearly pm^1 that was first lost, yet, on the other, the positions of the premolars in certain of the modern Phalangistidæ are such as to raise a suspicion that they also, like the Polyprotodonts, have lost pm^2 rather than pm^1; but in any case the loss has been independent of that in the Polyprotodonts, both groups having had four premolars some time after their separation from one another.

§ I have found this method of writing dental formulæ far superior to the ordinary one, as by it, not only the number, but the homologies of the teeth are clearly shown. Each tooth has its serial number, which is written in if the tooth is present, but is replaced by a cipher if not.

Perameles, and *Didelphys*, and from which again we obtain, by the disappearance of pm^4, that of *Dasyurus* and *Sarcophilus*, namely P.M. $\frac{1\,.\,0\,.\,3\,.\,0}{1\,.\,0\,.\,3\,.\,0}$.

Turning then to *Myrmecobius*, with its eight or nine cheek-teeth, of which only three are commonly reckoned as premolars, I examined several young specimens in order to see if this animal, like the abnormal *Phascologale*, had not really four premolars, as no exact observations on it had been published, and the usual determination rested merely on the shape of the teeth. In fact, even if no tooth-change could be found, it seemed possible enough that the small tooth commonly reckoned as the first molar should be really a persistent milk pm^4, the permanent tooth corresponding to it having become aborted.* This theory, however, I have been able to disprove by the examination of such a jaw as is shown in Plate 27, fig. 9. Here we find that, of the whole set of cheek-teeth (premolars and molars), the first, second, fourth, and fifth are fully up, and all much on a level with one another, while, on the other hand, the third has scarcely penetrated the gum, and stands therefore far below the level of the rest. Hence we see that this third tooth, by its very lowness of position, or rather lateness of development, is certainly the true pm^4, even without there being any milk-tooth above it; for, had it been pm^3, it would have been at all stages, as with other animals, fully on a level with the teeth next in front of and behind it. Of a milk-tooth preceding this pm^4 I can find no trace whatever, although it is possible that, considering the very rudimentary degree of development in which the milk-tooth occurs in the Thylacine and Koala,† it may yet be discovered in specimens younger than have yet been examined. The correct formula of the cheek-teeth of *Myrmecobius* is thus P.M. $\frac{1\,.\,0\,.\,3\,.\,4}{1\,.\,0\,.\,3\,.\,4}$, M. $\frac{1\,.\,2\,.\,3\,.\,4\,.\,5\,.\,0}{1\,.\,2\,.\,3\,.\,4\,.\,5\,.\,6}$; and therefore, so far as regards the premolars, identical with that of *Phascologale* and *Thylacinus*.

As regards the incisors, two specimens of *Myrmecobius* in the Natural History Museum present the interesting anomaly of possessing four instead of only three lower incisors, the extra tooth being in each case clearly i^4—a fact which proves what has generally been presumed to be the case, viz., that it is the fourth incisor that has disappeared in ordinary three-incisored Mammals.

This completes the list of the living Dasyuridæ to be referred to, but one fossil Marsupial, perhaps referable to the same family, and, although nearly the oldest-known Mammal, strongly resembling the modern *Phascologale*, has a dentition of so interesting a character as to call for special notice. This is the *Triacanthodon serrula*, described by Sir R. OWEN‡ from a single lower jaw found in the Mesozoic Purbeck

* A process which, as noted below, p. 451, has taken place in certain Placentals.

† THOMAS, 'Zool. Soc. Proc.,' 1887, p. 338.

‡ 'Mammalia of the Mesozoic Formations' (Palæontographical Society), 1870 (pub. 1871), p. 72, Pl. IV., figs. 7 and 8. Mr. LYDEKKER ('Catalogue Fossil Mammalia Brit. Mus.,' vol. 5, p. 258) considers this fossil as not generically, or even specifically, separable from *Triconodon mordax*, OWEN, described at the same time.

beds of Swanage, Dorsetshire.* An examination of this solitary lower jaw shows what is, considering the immense antiquity of the species, rather a startling fact, namely, that it had an absolutely identical tooth-change to that found in modern Marsupials. This fact is shown most clearly by the typical specimen, which happens fortunately to be in precisely the right condition to show it, namely, with the milk-premolar still in its place in the jaw, while the permanent pm^4 is clearly visible buried in the bone beneath (see Plate 27, fig. 10). The milk-premolar is not small and nearly functionless, as it is in *Phascologale*, but is nearly as large as, and is very similar in shape to, the first molar standing just behind it. This ancient and remarkable fossil gives us, therefore, the one stage earlier than the abnormal *Phascologale* above described, having, on the presumption that its upper jaw resembled its lower, the full premolar formula of P.M. $\frac{1 \,.\, 2 \,.\, 3 \,.\, 4}{1 \,.\, 2 \,.\, 3 \,.\, 4}$, all the teeth equally well developed, and the fourth one with a large and functional milk predecessor.†

We may now consider this history of the evolution of the premolars of the Dasyuridæ as fairly proved, and may represent it diagrammatically as follows :—

Fig. 1.

	P.M. 1	2	3	4	Process.	Examples.
I.	V	V	V	V U	Complete set	*Triacanthodon.*
II.	V	v	V	V U	Reduction in size of pm^2	Abnormal *Phascologale.*
III.	V	o	V	V U	Loss of pm^2	Ordinary *Phascologale.*
IV.	V	o	V	v	Reduction in size of pm^4	*Phascologale apicalis*, &c.
V.	V	o	V	o	Loss of pm^4	*Dasyurus* and *Sarcophilus.*

In this diagram the permanent teeth are represented under their respective serial numbers by a **V** if present, and by an **O** if absent, while the milk-tooth is similarly shown by a shaded **U** if present, but is altogether unrepresented if absent.

We will now pass from these details of individual species to the larger question as to the steps by which the primitive ancestral set of Mammalian teeth has become

* This specimen is also referred to by Professor FLOWER in an address to the Odontological Society ('Odontol. Soc. Trans.,' vol. 3, 1871, p. 220), and he there, on the then unverified assumption that it possessed a changing pm^4, made certain remarks on the probable direction of the evolution of a Diphyodont dentition—remarks which all the evidence at my disposal most fully bears out.

† As Professor FLOWER has pointed out in his paper just quoted, the type-specimen of *Triconodon occisor*, OWEN (figured *op. cit.*, Pl. IV., fig. 2), found in the same beds, also shows traces of having had a changing pm^4, the latter tooth being very markedly retarded in development, as if a milk predecessor had only just been lost from above it. There seems, in fact, to be every reason to suppose that all the Purbeck Polyprotodonts had a similar tooth-change, judging from such indications as may be gathered from the relative positions of the teeth.

modified into the very various forms of modern dentition, and especially as to the passage from the Marsupial to the Placental style of dentition.

The first and most fundamental question that arises is this :—Is the rudimentary tooth-change now found in the Marsupials the last remnant of a complete change present both in their ancestors and in those of the Placentalia, or does it represent an early stage in the first formation of such a complete change, the Marsupials being still in a backward condition, out of which the Eutheria have long ago passed?

To my mind it is perfectly clear that it is the second and not the first question that should be answered in the affirmative; although, so far as I can find, all the Continental and many of the English naturalists think the opposite—a view, however, that, although easy and obvious at first sight, I cannot for one moment believe to be correct. When we consider that in every character of their organisation the Marsupials are infinitely behind and at a lower stage of evolution than the Placental Mammals, it would appear to be a total subversion of all the ordinary rules to suppose that in this one character of their dentition they should have passed on in advance of all the other Mammals, and, having gone through the condition in which the latter now are, should have again nearly evolved away that process of tooth-change which is to its Placental possessors so evidently advantageous. It would be to my mind inconceivable that this should be the case, considering how universal among the Eutheria a more or less complete tooth-change is, and how useful it has proved to be to them, as evidenced by the very fact of their so wholly supplanting the more lowly organised Marsupials—more lowly organised in their dental as well as in their other characters, and not further advanced, as would have to be presumed were their teeth looked upon as a later development of a fully Diphyodont set.

And again, the mere fact that five out of the six families of Marsupials, natives both of Australia and America, have, with the comparatively unimportant exceptions already noted as occurring among the Dasyuridæ, arrived at precisely the same stage of tooth-change is itself a very strong argument in favour of the view now advocated; for, were the modern tooth-change a remnant of a fuller one, we should naturally expect that, under the very various conditions of the struggle for existence, equally various degrees of reduction would have been attained to. On the other hand, we should be most unlikely to find, as is now the case, more than 90 per cent. of the existing and fossil Marsupials changing one single tooth, and one only, and the small remainder merely differing from them in a direction away from and not towards that fuller tooth-change of which it is said their ancestors were once possessed.

Of the one form of evidence needed to give any weight to the opposite theory, namely, that derived from Palæontology, there seems not to be one atom, no fossil Marsupials having ever been found showing traces of a larger amount of tooth-change than the recent ones, nor do I think such a discovery likely to be made, as, to the best of my belief, no such animal has ever existed. This view is very much strengthened by the fact that, as already noted, one of the oldest Mammals known,

the Mesozoic *Triacanthodon*, had precisely the same, and no more, tooth-change than the modern Marsupials.

For these various reasons, therefore, we may, I think, take it for granted that the ancestors of the Marsupials never had at any time a more complete change of dentition than they have now, and that they arrived at their present state at an immensely early period, since which time they have as a whole practically stood still, except that a few isolated forms have, comparatively recently, lost again even the small amount of change they once possessed.

The second question, and one equally vital, is as to whether the milk set of teeth is the original primary set with the permanent one superadded to it, as believed by many naturalists, and especially by embryologists, or *vice versâ:* a question with which Professor FLOWER has dealt in the first of his papers above referred to.* His conclusion was that the permanent dentition was the original one, and that the milk set had been afterwards developed as an addition to it—a view to which, although inclined at first to disagree, I have now become a firm adherent. To this opinion I have come by finding the impossibility of working out the general homologies of the teeth on the basis of the opposite view, and by the comparison of an infinitely larger number of specimens of various sorts than even Professor FLOWER had access to. The chief cause of the prevalence of the opinion that the permanent dentition is a later development than the milk is the deceptive appearance presented in the early stages of tooth-development, when the germ of the permanent tooth is first seen as a bud growing out from that of the milk-tooth, whence it has naturally been supposed that the latter was the primary and the former the secondary development. Even should this appearance of budding off, however, be entirely correct—and the fact itself is strongly denied by R. BAUME†—it may be argued that, considering the uniform direction of the evidence drawn from later stages, there is no sufficient reason to deny the possibility of a secondary organ, whose very *raison d'être*, as in the case of the milk-tooth, is its speedy and precocious development, so overshadowing in size and rapidity of growth what is really the primary as to make the latter appear as its bud, and therefore, although falsely, as a secondary and subsidiary growth.

A second, apparently adverse, argument may be drawn from the few instances known of milk-teeth‡ developed, and remaining through life, without having, or only rarely having, true permanent successors, as in the anterior premolars of the Proboscidea § and some of the Perissodactyla, ‖ but these are clearly due to the teeth

* 'Phil. Trans.,' 1867, p. 639.

† 'Odontologische Forschungen: Versuch einer Entwickelungsgeschichte des Gebisses,' 1882, p. 75.

‡ *I.e.*, the homologues of the corresponding milk-, and not permanent, teeth in the allied species.

§ R. LYDEKKER, 'Cat. Foss. Mamm. Brit. Mus.,' Part 4, 1886. (*Introduction*, p. vii.)

‖ R. LYDEKKER, 'Bengal, Asiat. Soc. Journ.,' vol. 49, 1880, p. 135. This interpretation by Mr. LYDEKKER of the homologies of the non-changing pm^1 in the Rhinoceroses has been called in question, but his evidence, drawn from an abnormal Rhinoceros skull in the Calcutta Museum, seems to me to be fully sufficient to support the conclusions he came to—conclusions with which all the specimens that I have seen quite agree.

having passed through a complete cycle of evolution, the "permanent" tooth first developing, then having a milk-tooth superadded to it, and finally aborting itself and leaving its milk representative still persistent.

These two questions answered, we come to the consideration of the phenomena observable during the growth of a milk-tooth above its permanent successor; not the early and embryological ones, into which I do not propose to enter, but such as may be studied on the rich material of skulls of different ages available to me in the collection of the Natural History Museum.

Taking now the skull of a tooth-changing Marsupial in which the first teeth are just appearing, we see that the single milk-premolar* comes up at about the same time as the true permanent premolars anterior to it; that the first molar quickly succeeds and the other molars follow, but that almost invariably, whether there is a change or not, the true pm^4 is considerably later in its development than the other teeth, and, especially, than either pm^3 or m^1. In the original production, therefore, of a milk-tooth above one of the other teeth, say pm^3, whose summit is, to commence with, fully equal in height at all stages of development to the summit of the milk-tooth of pm^4 standing just behind it, we see that a change of position is necessary in this pm^3 before a milk-tooth can be developed over it, a change which can apparently only be brought about by the retardation of its growth, and its approximation thereby to the state in which pm^4 now is.

Should this supposition be true, we should expect to find that, anterior to the first appearance of a milk-tooth in any group, specimens would be found showing a preliminary retardation of the individual teeth over which, in a later generation, milk-teeth were to be developed. The difficulties in the way of understanding how the ordinary processes of evolution can have first brought about such a preliminary retardation are, of course, considerable, unless it be that the retardation is itself a favourable character, by its preventing the undue crowding of the young animal's mouth, while, at the same time, the full number of teeth are developed for use by the adult. In this case it would be comparatively easy to understand the assumption of a milk dentition by the two steps, each favourable in itself—(1) of a retardation for packing purposes of the permanent tooth in some large-toothed form, followed, in a later generation, by (2) the temporary development of a deciduous tooth in one of its descendants with the teeth so small that the gap in the tooth-row during youth, inherited from large-toothed ancestors, had become a defect to be remedied in this most effective manner.

Turning now to the actual facts, we find that there is among the Marsupials a

* It seems better to use this term rather than "milk-molar," as the milk-teeth have nothing to do with the true molars, and that name is, therefore, productive of constant confusion. And, again, the use of the word "deciduous" instead of "milk" seems to be inadvisable, as both the molars and premolars of the second set are often themselves deciduous, while occasionally those of the first or milk set remain throughout life.

hitherto unnoticed, but most striking and peculiar, retardation in the development of the first upper incisors in all the three Polyprotodont families, these families being the very ones in which, as the incisors are not so specialised in another direction as are those of the Diprotodonts, we should most expect to find traces of the development of milk incisors. In half-grown specimens, such as those of *Sarcophilus ursinus* and *Phascologale wallacei* (figured Plate 27, figs. 11 and 12), at a time when the three outer incisors are fully up and in use, the first pair, the largest in the adult (*Ph. wallacei*, fig. 13), are still quite minute, with their points only just projecting above the bone, and altogether in a very marked condition of retardation. And the same appears to be the case in young specimens of Didelphyidæ, Peramelidæ, and other Dasyuridæ, in many of which the first incisors in the fully adult animal are by far the largest of all. The theory now suggested, therefore, about these Marsupials with retarded first incisors, is that they represent at the present day the stage at about which the common ancestors of the Metatheria and Eutheria diverged from each other—a stage when the teeth were, as it were, preparing themselves for the assumption of milk predecessors, a process which has in the latter group been continued onwards until the complete Diphyodont condition has been attained. On the other hand, in the former the process has, except in the case of pm^4, never gone beyond the initial stage of the retardation of i^1, a stage which has itself been continued owing to its own inherent value.

For this view as to the first incisors it may also be urged that the most likely of all the teeth to undergo a marked alteration of any sort would be those at the extreme ends of the series, judging by the manner in which, throughout the Mammalia, the first incisor and the last molar show themselves plastic in readily taking on characters not, or only much later, found in the neighbouring teeth.

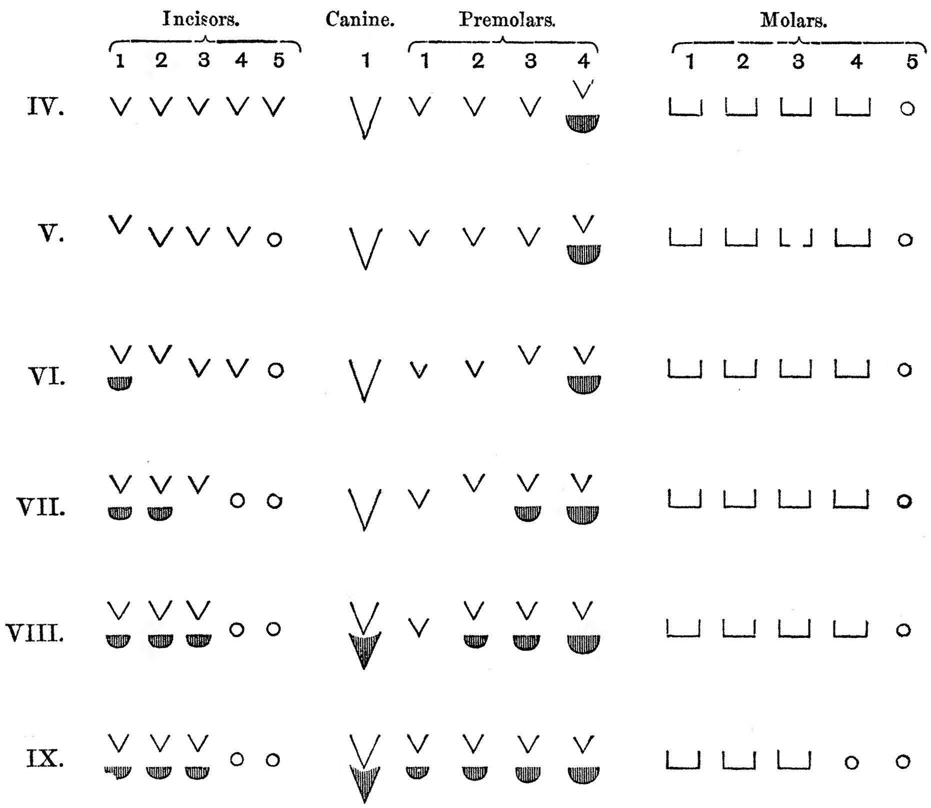
Before leaving this subject, I would wish to point out that it is by no means essential to the general views here advocated that this suggestion as to the first incisors should be correct, but only that, as some tooth or other must have been the first to follow the example of pm^4 in developing a milk predecessor, the first incisor, even apart from its retardation, is at least as likely as any other to have been that tooth, while on this theory we also gain a possible explanation of the same very curious retardation. Should, however, future palæontological research show that any other tooth, say the canine or pm^3, took on a milk predecessor before i^1, it would only disprove the present suggestion without in any way invalidating the general conclusions come to.

In order now to put into order the various suggestions above made, and to utilise them for the purpose of making out the past history of tooth evolution, we will commence by drawing up diagrams on the same principle as in fig. 1, but the whole set of teeth, instead of only the premolars, is taken into account (fig. 2).* Here IV.

* In these diagrams and their explanations the teeth of the upper jaw only are referred to, as it is there alone that, owing to the presence of the premaxillo-maxillary suture, the true relations of the

represents a generalised Marsupial dentition with five incisors,* four molars, and four premolars, of which the last is retarded, and has a milk-tooth superadded to it. The next advance on this in the Placental direction would be V., obtained by the retardation of i^1 and the suppression of i^5, a stage exactly represented in the abnormal *Phas-*

Fig. 2.



cologale above described. Then, if the above theory is correct, should follow, first, VI.,† where the retarded i^1 has developed a milk predecessor, and i^2 and pm^3 are retarded; secondly, VII.,† in which the development of milk-teeth has extended from in front backwards and from behind forwards, and i^4 has dropped out; and, thirdly, VIII., which would be just such a generalised Placental dentition as is now possessed

teeth can be made out with certainty. But whatever changes the upper teeth have passed through must of necessity have also been undergone, *pari passu*, by the lower.

* As in *Didelphys* and some *Perameles*.

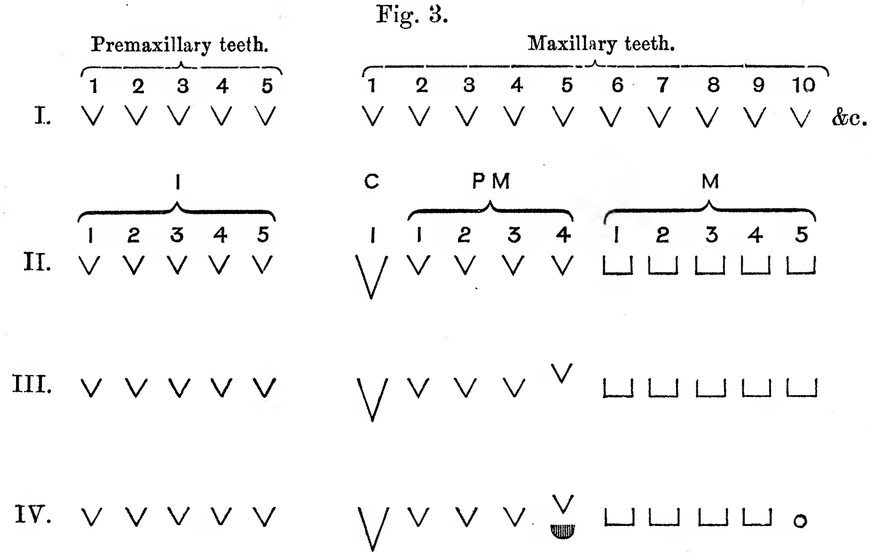
† Some of the ramifications of these intermediate stages *may* be represented by certain of the Eocene Creodonta of North America, as, for example, by *Triisodon quivirensis*, Cope, 'American Naturalist,' vol. 15, 1881, p. 667 (figured *op. cit.*, vol. 18, 1884, p. 257), which is said to have changed its two posterior premolars only, but the published descriptions of this interesting fossil and its allies are so incomplete and confusing that it is difficult to obtain any exact idea of their dental characters. It must also be noted that, although Professor Cope looks upon and argues from *Triisodon* as an animal only changing its pm^3 and pm^4, there appears to be no evidence that it did not also change its pm^2, canine and incisors, like *Hyænodon* and the Carnivora of the present day.

by *Otocyon*,* viz., three incisors and one canine, all changing; four premolars, of which the last three change; and four molars. Finally, IX. is the still further development shown in the Tapir, Hyrax, and one or two other forms, in which pm^1 also changes, and, as in the vast majority of Placental Mammals, m^4 is lost.

If, now, we attempt in the same manner to trace the history of the tooth-changes upwards to the earlier forms from the Marsupial dentition, instead of downwards to the later ones, we obtain a diagram as follows :—

Here IV. is, as before, the generalised Marsupial dentition, as already described. III. would then be the stage preceding it, where one or more additional posterior molars are still habitually retained, and where the milk predecessor to pm^4 has not yet been developed, although that tooth is in the preliminary stage of retardation. In II. we get back to a condition in which the teeth are about equal to one another in

Fig. 3.



their rate of development, none being retarded, and only show a commencement or first sketching out of the division into canines,† premolars, and molars by a lengthening of the anterior and a broadening of several of the posterior maxillary teeth. Finally, in I. the teeth would have been of a purely homodont character, only divisible into five premaxillary and a variable number of maxillary teeth. Of these maxillary teeth, it would seem to have been generally the fifth ($= pm^4$) which first developed a milk predecessor, and thereby became, with the three non-caniniform teeth in front of it, a "premolar." Where the maxillary teeth exceeded nine, the increase

* Whether this animal has returned to, or retained, its ancestral number of molars is still doubtful, but it presents, in any case, an interesting example of a stage of dentition through which the line of Placental Mammals must have passed. (*Cf.* HUXLEY, 'Zool. Soc. Proc.,' 1880, p. 256 *et seq.*)

† Although, as urged by MOSELEY and LANKESTER ('Journ. Anat. Physiol.,' vol. 3, 1869, p. 73), the canine is not essentially a distinct tooth from the premolars, yet it was evidently very early specialised, as is shown by such forms as the Mesozoic *Stylodon pusillus*, OWEN.

appears to have been wholly in the number of the true molars, and not of the pre molars, as is particularly well illustrated by the early representatives of the many-toothed Odontocete Cetacea,* and also by the great majority of the Mesozoic Mammalia, many of which,† while still having only four premolars, have from five to eight true molars. In fact, the earliest forms seem to have normally had a considerable number of molars, but these were soon reduced down to four in the Metatheria, and later to three or less in the Eutheria, leaving a few isolated forms,‡ with larger numbers as remnants, retaining what the common ancestors of all had once possessed. Two only of the many described genera of these ancient forms have been said to have more than four premolars, namely, *Amphitherium* and *Amphilestes*, each described as having six premolars and six molars§; but, as even this determination is disputed,‖ and in any case rests entirely on the form of the teeth, and not on a knowledge of their manner of changing, it can hardly be said to prove incorrect the practically universal rule that the typical number of premolars is, and has always been, at least since middle Mesozoic times, four, and four only.¶

Whether the teeth in the first stage of all were rooted or rootless is very doubtful, but the probability seems to be on the whole that they were simple conical teeth, rootless for part, if not the whole, of the animal's life, and possibly not unlike those now possessed by some of the Dasypodidæ.**

This first stage in the Mammalian dental series would probably very fairly represent, so far as can be judged, the dentition of the Prototheria, the toothed and generalised ancestors of the living, and now highly specialised, Monotremata, which there is every presumption for believing, as Professor FLOWER has pointed out,†† were for some time both Homodont and Monophyodont.

If we now combine these diagrams and tabulate the various processes and examples already described, we obtain (Plate 28, I. to IX.) a complete diagram of the tooth

* *E.g.*, *Squalodon*, which has the following formula:—I. $\frac{3}{3}$ C. $\frac{1}{1}$ P.M. $\frac{4}{4}$ M. $\frac{7}{7} \times 2 = 60$. FLOWER, 'Encycl. Brit.' 9th edit., Article "Mammalia."

† *E.g.*, *Achyrodon manus*, *Stylodon pusillus*, &c. See OWEN, 'Mesozoic Mammalia' (Palæontogr. Society, 1870), 1871. Plate 2, figs. 6, 14, and 17.

‡ *E.g.*, *Myrmecobius*, *Bettongia*, which has not infrequently five true molars, and the many-toothed Edentates.

§ OWEN, *loc. cit.*, Plate 1, figs. 21–23.

‖ LYDEKKER, 'Cat. Foss. Mamm. Brit. Mus.,' Part 5, 1887, p. 271, footnote.

¶ A single instance is, however, known to me of a true Heterodont and Diphyodont Mammal with five premolars, namely, *Rhinogale melleri*, GRAY, a member of the Herpestine section of the Viverridæ. Of this remarkable species, however, only one skull is as yet known (figured 'Zool. Soc. Proc.,' 1864, p. 574), so that no positive deductions can be drawn from it. It may be either that the supernumerary premolar is a mere accidental duplication of one of the other premolars, or that one of the milk-premolars has been retained in position, but these points can only be settled by the examination of further specimens of the species.

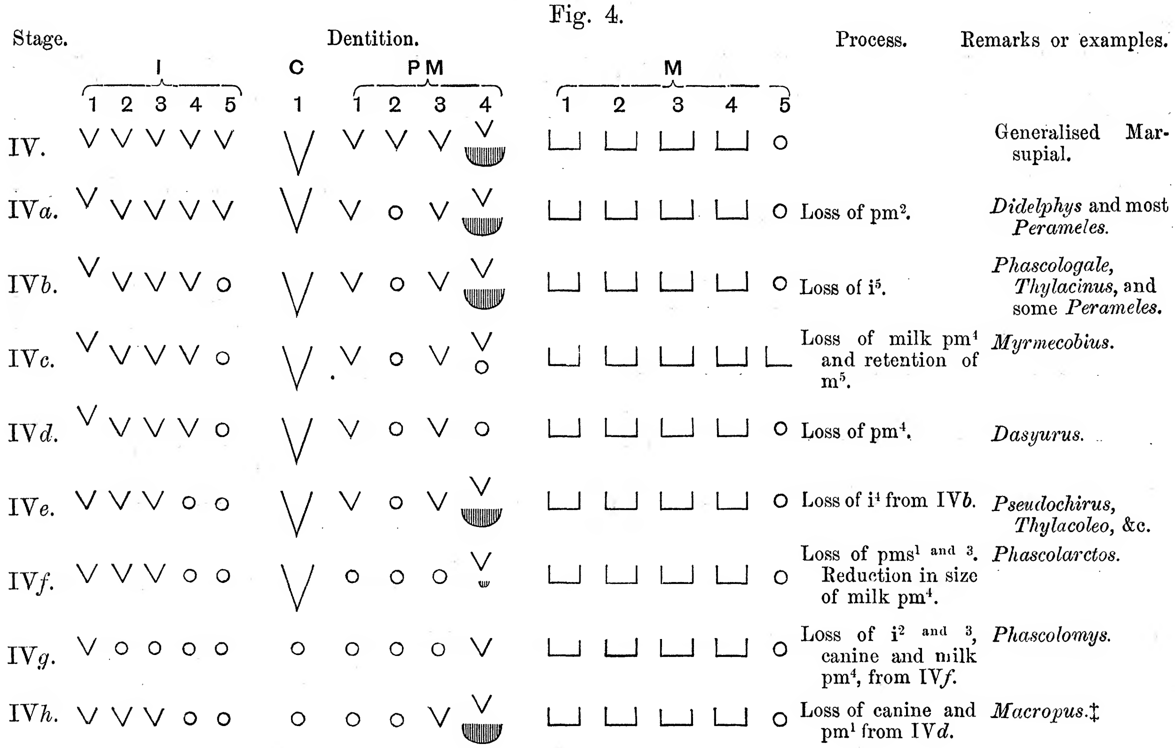
** See BAUME, *op. cit.*, p. 152, &c.

†† 'Odontol. Soc. Trans.,' vol. 3, 1871, p. 221.

changes that have taken place from the earliest Prototherian form (I.) down to such a fully developed Diphyodont dentition as is now possessed by *Tapirus* (IX.), from which again, or more directly from VIII., there have arisen, by the different processes of tooth variation, all the numerous forms of modern Eutherian dentition as exemplified on the diagram by X. (*Elephas*),* XI. (*Hydromys*), XII. (*Felis*), or XIII. (*Chiromys*).†

Again, working in another direction, we can obtain an idea of the tooth evolution that has taken place in the Marsupials by starting from the "generalised Marsupial"

Fig. 4.



stage represented by IV. in figs. 1 and 2, at which point the direct evolution of Diphyodontism was in their case arrested, and drawing up a similar diagram (fig. 4) to those already given. This diagram, however, is quite simple, and only depends on the loss or variation of individual teeth, and therefore does not need any detailed explanation beyond what is placed under the headings of "Process" and "Remarks" in the diagram itself. The position of this line of dental evolution in the general system is shown on Plate 2 under the heading of "Metatherian branch."

* No evidence as yet exists as to which of the three incisors is represented by the Elephant's tusk, which is here only provisionally called i¹.

† See PETERS, 'Berlin, Akad. Abhandl.,' 1865 (*Phys.*), p. 79 *et seq.*, Pl. 2.

‡ Of course it is not pretended that the dentitions of these animals are directly descended from one another, but the diagram serves to show by what steps any individual dentition may have been evolved from the generalised type.

Of the other Mammalian orders all fall easily enough into their places in this scheme,* with two exceptions, namely the Cetacea and Edentata. As regards the first, the general drift of the evidence seems to be that their ancestors have passed through a stage with a more or less complete milk dentition, which has gradually been again aborted,† its place being taken in the Odontocetes by the large and quasi-vegetative increase in the number of the molars, and in the Mystacocetes by the baleen, which latter has so fulfilled all the requirements of the animal that the "permanent" or original dentition has also been reduced to the position of a useless atavism, shed or absorbed before birth, and not playing any functional part in the life of the animal.

In the Edentata, on the other hand, we find, as is well known, characteristics wholly at variance with those of all other Mammals. In fact, a study of the teeth of this

Fig. 5.

Stage.	Dentition. Premaxillary teeth. 1 2 3 4 5	Maxillary teeth. 1 2 3 4 5 6 7 8 9	Process.	Remarks and examples.
α	V V V V V	V V V V V V V V V		Generalised Mammal (Stage I. of fig. 3).
β	o o o o V	V V V V V V V V o	Loss of i^{1-4}.	*Dasypus.*
γ	o o o o o	V V V V V V V V (V)	Loss of i^5.	*Xenurus*, &c.
δ	o o o o o	V V V V V V V V V , &c., up to 25	Increase of number of molars.	*Priodon.*
ε	o o o o o	V V V V V o o o o	Decrease of number of molars.	Bradypodidæ, Megatheriidæ.
ζ	o o o o o	o o o o o o o o o	Total loss of teeth.	Myrmecophagidæ, Manidæ.
η	o o o o o	V V V V V V V V o	Assumption of milk-teeth.	*Tatusia.*

order soon induces a belief that the variance is so great as to preclude the possibility of the Edentates lying within the same lines of development as other Mammals, a belief that tallies exactly with the conclusions of Professor PARKER,‡ drawn from the embryology of the group.

With this idea we may look upon the dentition of the Edentates as also based, like that of other Mammals, on Stage I. of the diagrams (fig. 3, and Plate 28), but modified in a different direction, and one peculiar to itself. Working out this suggestion, as before, by means of diagrams, we have the same Stage I. (fig. 5, α), in which the teeth are simple, and only divisible into five premaxillary and a variable number of maxillary

* Except that, of course, innumerable problems still remain to be settled as to which of the typical number of teeth are present or have disappeared in the different groups. This is, however, merely a matter of detail, and does not affect the scheme in general.

† *Cf.* FLOWER, 'Journ. Anat. Physiol.,' vol. 3, 1869, p. 271.

‡ 'Phil. Trans.,' 1885, p. 116. 'Mammalian Descent,' p. 97, 1885.

teeth. Then, with merely the slight modification of the loss of the first four premaxillary teeth, we get β, the dentition of *Dasypus;* next, by the suppression of the last premaxillary tooth as well, we obtain γ, that of *Xenurus, Tolypeutes,* and *Chlamydophorus.* Then, on the one hand, a simple increase * of the number of the maxillary teeth to 20 or more results in δ, the dentition of *Priodon,* and, on the other, a similar decrease to 5 in that of *Bradypus* and its allies, both recent and fossil (ϵ). This reduction is then carried out to its extreme in *Myrmecophaga* and *Manis* (ζ), both entirely toothless. Finally, η based on γ, with the superaddition of a nearly complete set of milk-teeth, gives us the remarkable and unique double dentition of the genus *Tatusia.*

Should this view of the derivation of the Edentata be correct, it is evident that their line of development should have a name corresponding to the useful evolutionary terms suggested by Professor HUXLEY† for the great Mammalian groups, and since almost universally used. I would, therefore, altogether remove the Edentates from the "Eutheria" and call them the "Paratheria," to indicate their position by the side of, but separate from, the other Mammals.

One genus of Edentates has not been mentioned, namely *Orycteropus,* with its extraordinary canaliculated compound teeth, wholly unique among Mammals, and only comparable to those of certain Fish. I can, however, at present make no suggestion as to the origin or evolution of these teeth, there being as yet no evidence bearing upon them in any way.

Putting now together all the diagrams above worked out, we obtain the general genealogical Table (Plate 28), in which the three great lines of development are shown, viz., the main Proto-meta-eutherian stem, I. to XIII., at the bottom of which all the modern Placentals stand; I.–α to I.–η, the Edentate or Paratherian line; and I. to IV., and from IV. to IV.–h, that of the Marsupials.

The influence that these theories, if correct, will exercise on tooth-notation is a matter of detail which will require proper working out in each group; but it is evident that such generalisations as that missing incisors are always gone from the posterior and missing premolars from the anterior ends of the series are quite untenable, and that every group must have the homologies of its teeth worked out for itself, and not merely put down under the influence of any such general rule. This influence has even caused such eccentricities as the numbering of the premolars from behind forwards, a proceeding which would, for example, result in the two premolars of *Dasyurus* being called (from before backwards) pm^2 and pm^1, instead of, as they have above been shown to be, pm^1 and pm^3 respectively.

Having now put forward the views gained by my own examination of specimens, there remains to be noticed the other published work on the subject. The numerous contributions to the history of teeth made by Sir RICHARD OWEN during the last 50

* Or, perhaps, rather a retention of the numerous teeth no doubt possessed by the earliest Prototheria.

† 'Zool. Soc. Proc.,' 1880, p. 653 *et seq.*

years are so well known as to need no more than a passing mention from me. In all questions of fact, especially in connection with the fossil forms, I have gained great assistance from them, an assistance for which I must make my due acknowledgment. Of Professor FLOWER's papers, already referred to, it need only be here remarked that every opinion he expressed has been fully confirmed, and that any advance on his papers is due to the examination of a far larger series of specimens than were available to him—an examination carried out very largely on the lines indicated by him. To Mr. C. S. TOMES's invaluable work, 'Dental Anatomy,' I am also largely indebted for information in regard to the growth and early development of the teeth.

Of the more recent foreign contributions to the subject, the most important are those of Professor E. D. COPE* and of Dr. R. BAUME†; but the differences between their views and those now brought forward are so considerable, and involve so much detailed argument, that a criticism upon them would here be out of place. It must, therefore, suffice to say that their respective views on the descent and homologies of teeth have been fully taken into consideration during the preparation of the present paper.

In conclusion, as it is to the general advantage that true theories should be confirmed and untrue ones soon exploded, I have thought it useful to draw up a few notes on the possible or probable discoveries relating to this subject, in order that they may be looked for and their true bearing understood by persons interested in, and having opportunities for making observations on, tooth-homologies.

1. The discovery in a recent Marsupial of a milk-tooth preceding one of the permanent set other than pm^4, and especially i^1. This discovery, although unlikely to be made, would on the whole be confirmatory of the views above advocated, as it would show that the process of the formation of milk-teeth is still going on in the Marsupials on the lines believed to have been followed by the common ancestors both of them and of the Eutheria.

2. The same in a fossil, undoubtedly Marsupial, and in its other characters allied to, and perhaps ancestral to, the living forms. This would be obviously entirely fatal, as it would show that the view as to the Marsupial tooth-change being a remnant and not a commencement of a full change is, after all, the true one. On the other hand, it is just possible that some of the extinct Marsupials may have antedated the existing species in the formation of a fuller milk dentition, and have then died out from some unexplained cause. A full, and not a rudimentary, tooth-change in a fossil Marsupial would, therefore, be the best and most final disproof of my views. That such a discovery, however, will ever be made, I cannot believe, especially considering the astonishing persistence of precisely the same amount of tooth-change from the Mesozoic to the modern Marsupials.

* Papers in the 'American Naturalist,' 'Proceedings of the American Philosophical Society,' and elsewhere.

† 'Odontologische Forschungen.—Versuch einer Entwickelungsgeschichte des Gebisses,' 1882.

3. Fossil Eutherian Mammals, showing an intermediate degree of tooth-change between the modern Eutheria and Metatheria, would obviously be highly favourable to the views now put forward as furnishing some of the intermediate stages corresponding to those above called Stages VI. and VII.

4. The discovery of a rudimentary *successor* to any of the premolars or other teeth now unchanging in the Marsupials. This also would be fatal, as it would show that it is, after all, the permanent and not the milk set of teeth which is superadded. It is, however, possible that at the first commencement of the assumption of a fuller change by the Marsupial ancestors of the Placental Mammals the Marsupial characters of inflected jaw, imperfect palate, &c., were retained for some time after the rudimentary tooth-change had been improved upon. In some Mesozoic fossils, therefore, the Metatherian osteological and Eutherian dental characters may be found to have co-existed for a certain time without invalidating the views above expressed.

5. Fossil Edentates with more premaxillary teeth than one, or, in other groups than true *Dasypus*, with any at all, would be confirmatory of the suggestion that the Edentates descended from the same Stage I. as other Mammals, and had lost four, or all, of their original number of five premaxillary teeth.

6. Further instances of the atavistic recurrence of usually absent teeth in all groups of Mammals are much needed for the working out of the tooth-homologies in the different groups.

On any of these points it will be most important to have information, and I hope that such, whether favourable or adverse to my views, will, if correct and properly authenticated, be soon forthcoming.

Explanation of the Plates.

PLATE 27.

Fig. 1. Anterior cheek-teeth of *Phascologale virginiæ*.
Fig. 2. ,, ,, ,, *penicillata*.
Fig. 3. ,, ,, ,, *thorbeckiana*.
Fig. 4. ,, ,, ,, *apicalis*.
Fig. 5. ,, ,, *Dasyurus viverrinus*.

This series shows the gradual decrease in size, and ultimate loss, of the last premolar (pm^4).

Fig. 6. Anterior cheek-teeth of *Phascologale penicillata*, showing the milk pm^4 in position, and its successor above it still buried in the bone.

Fig. 7. Anterior cheek-teeth, left side, of abnormal specimen of *Phascologale dorsalis*, showing atavistic second premolar (pm^2) in position.

Fig. 8. Reversed drawing of the right side of the same specimen, to show the relative positions of the teeth.

Fig. 9. Lower jaw of *Myrmecobius*, showing retarded eruption of pm^4.

Fig. 10. Lower jaw of *Triacanthodon serrula*, showing the germ of the permanent pm^4 buried in the bone (*after* OWEN).

Fig. 11. Front of upper jaw of a young *Sarcophilus ursinus*, showing retarded development of the first incisor.

Fig. 12. The same in *Phascologale wallacei.*

Fig. 13. Adult *Phascologale wallacei*, showing relative size of first incisor when fully developed.

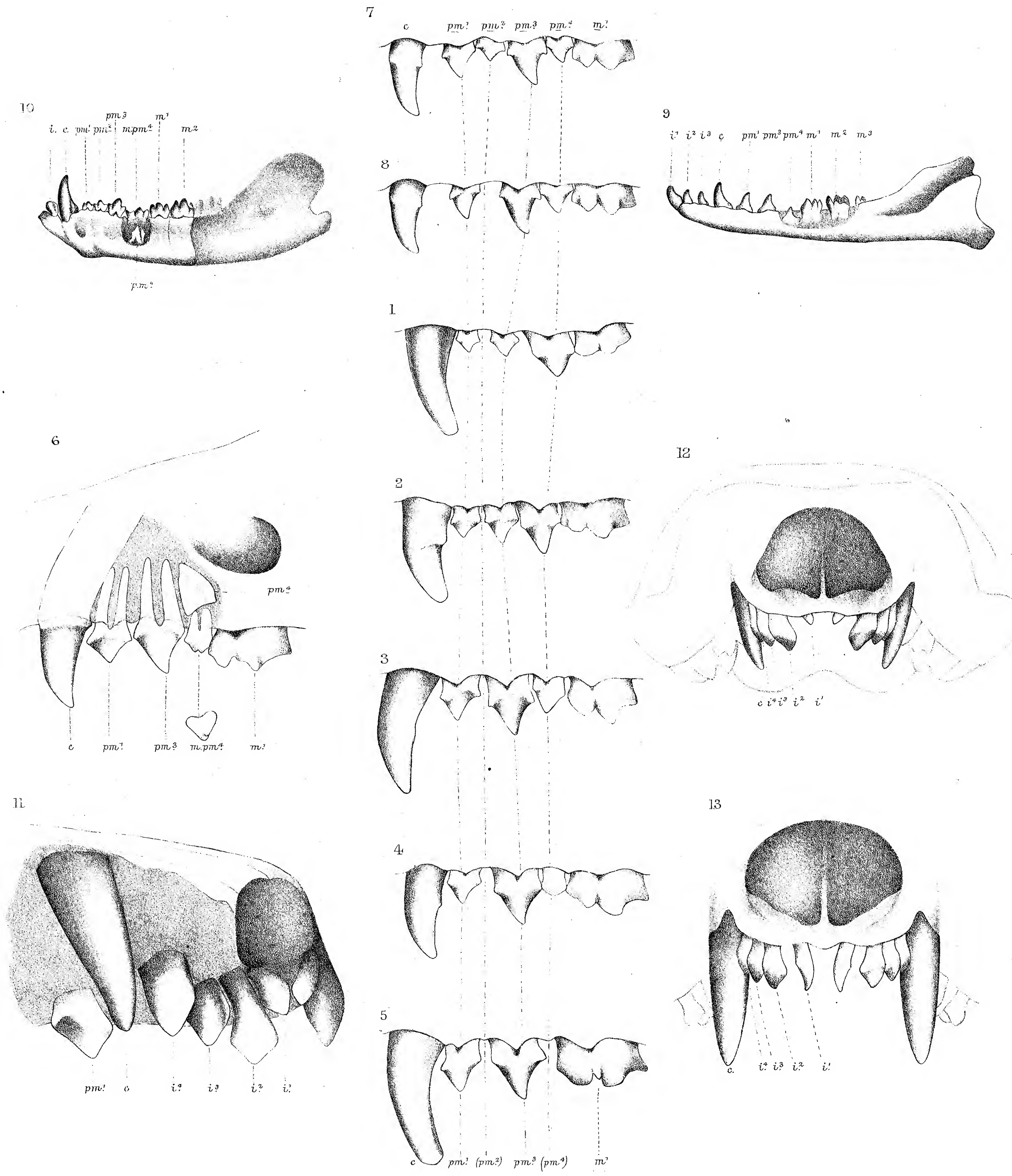
PLATE 28.

Diagrammatic representation of Mammalian tooth-evolution. On the right is the main stem of evolution, from the Prototherian to the Eutherian dentition. On the left, above, is the Paratherian (Edentate), and below, the continued Metatherian branch.

Main Stem.— I. Generalised Prototherian dentition.
II. and III. Intermediate stages towards—
IV. Generalised Metatherian dentition.
V., VI., and VII. Intermediate stages towards—
VIII. and IX. Generalised Eutherian dentitions.
X. to XIII. Examples of specialised Eutherian dentitions: X., *Elephas;* XI., *Hydromys;* XII., *Felis;* XIII., *Chiromys.*

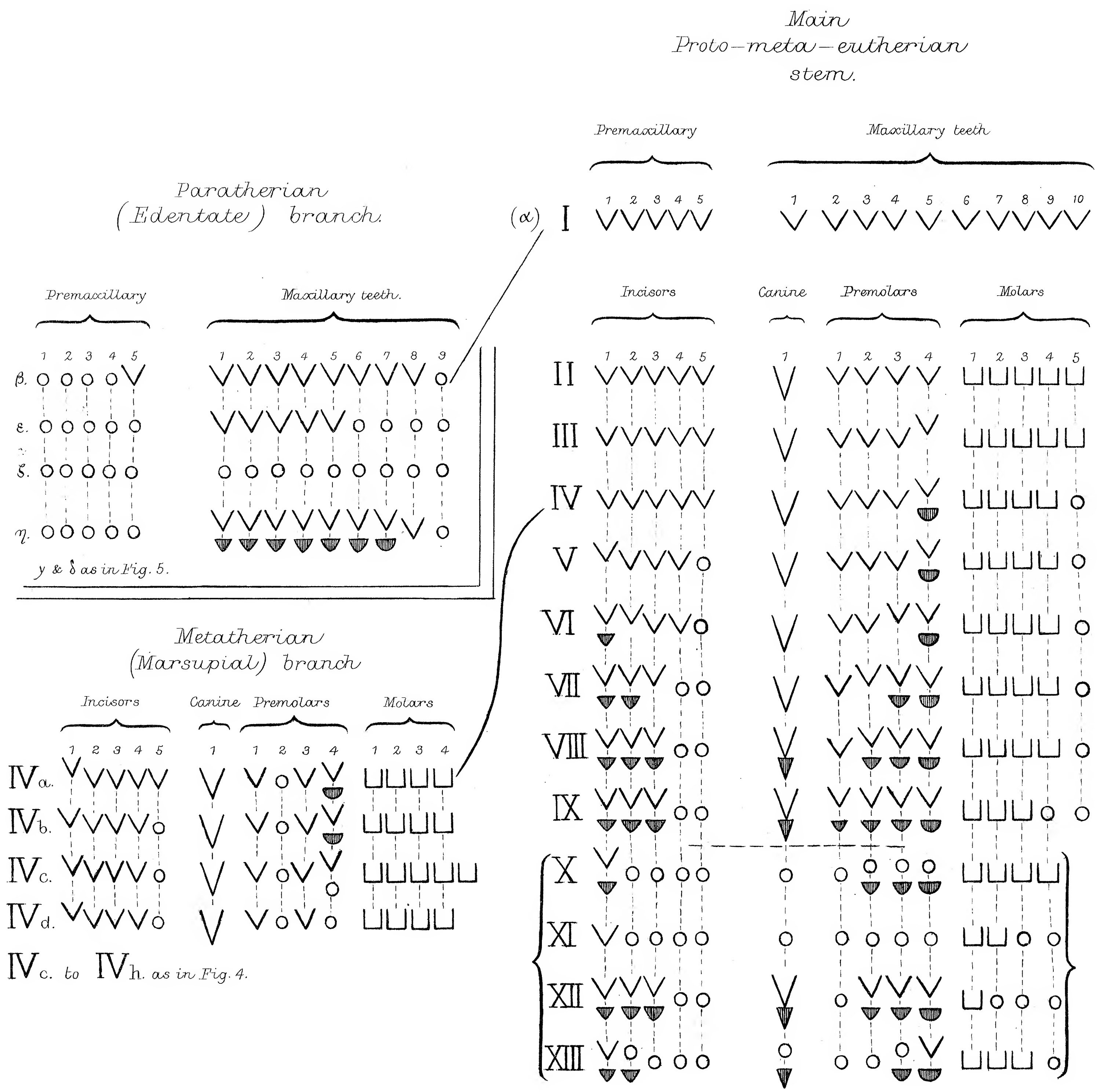
Paratherian Stem.—Starting from I. or α, the generalised Prototherian dentition.
β, *Dasypus;* ϵ, Bradypodidæ, Megatheriidæ; ζ, Manidæ and Myrmecophagidæ; η, *Tatusia.*

Metatherian Branch.—Starting from I., the Prototherian, to IV., the generalised Metatherian dentition.
IV. *a. Didelphys*, and most *Perameles.*
IV. *b. Phascologale, Thylacinus*, and some *Perameles.*
IV. *c. Myrmecobius.*
IV. *d. Dasyurus.*



M.H. Fisher, del. et lith.

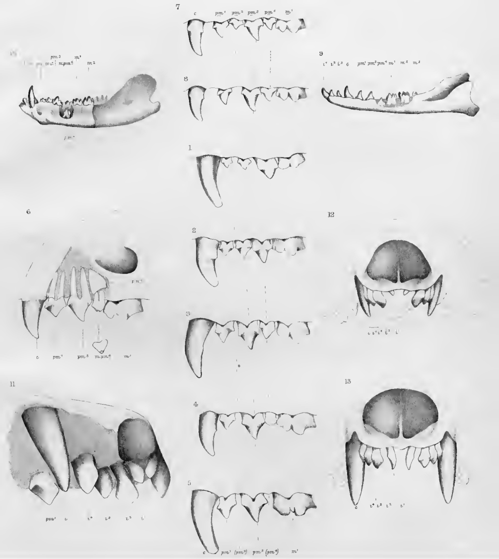
West, Newman & Co. imp



Main Stem.— I. *Generalized Prototherian dentition.* II & III. *Intermediate stages.* IV. *Generalized Metatherian dentition.* V–VII *Intermediate stages.* VIII & IX. *Generalized Eutherian dentition.* X. *Elephas.* XI. *Hydromys.* XII. *Felis.* XIII. *Chiromys.*

Paratherian branch.— β. *Dasypus.* ε. *Bradypodidæ, &c.* ζ. *Manidæ, &c.* η. *Tatusia.*

Metatherian branch.— IVa. *Didelphys, &c.* IV.b. *Thylacinus, &c.* IV.c. *Myrmecobius.* IV.d. *Dasyurus.*



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